Dimorphic cypsela germination and plant growth in *Synedrella nodiflora* (L.) Gaertn. (Asteraceae)

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(With 4 figures)

Abstract

Synedrella nodiflora is a weed species that has dimorphic cypselas: winged peripheral and lanceolate shaped central. The aim of this work is to describe the reproductive capability by measuring dimorphic cypselas morphology, imbibition rates and germinative patterns under temperature, light quality and water availability gradients, and compare the plant growth between two light treatments. The central cypselas were lighter, longer and its pappi were more elongated than the peripheral ones, favoring its dispersion. Neither type had deep dormancy and both of them germinated with the same pattern under the optimum conditions. Both cypselas showed higher germinability in temperatures between 25 and 30 °C, under white light and high water availability, although there are some differences between the types, mainly at dark treatments. Plants grown in direct sunlight accumulated more biomass, allowing for higher plant development and inflorescence production, although shaded light plants capitulum had a higher central: peripheral ratio than the direct sunlight treatment. *S. nodiflora* cypselas germinate better in unfiltered light places, although the plants are adapted to shady conditions. The species showed high germination potential over a wide range of environmental conditions, as well as fast plant development. All of these features favor distribution in environmental sites.

Keywords: achene, weed, osmotic potential, light quality, temperature.

Germinação de cipselas dimórficas e crescimento de plantas de *Synedrella nodiflora* (L.) Gaertn. (Asteraceae)

Resumo

Synedrella nodiflora é uma planta daninha que possui cipselas dimórficas: periférica alada e central com forma lanceolada. O objetivo deste trabalho foi caracterizar a capacidade reprodutiva por medição da morfologia das cipselas, taxas de embebição e padrões germinativos sob gradientes de temperatura, qualidade de luz e disponibilidade de água, e comparação do crescimento das plantas sob dois tratamentos luminosos. As cipselas centrais foram mais leves, compridas e seus pappi foram mais alongados que as periféricas, o que favorece sua dispersão. Nenhum dos tipos exibiu dormência profunda, germinando sob o mesmo padrão nas condições ótimas. Ambas as cipselas apresentaram maior germinabilidade sob temperaturas entre 25 e 30 °C, sob luz branca e alta disponibilidade hídrica, apesar de haver algumas diferenças entre os tipos, principalmente em tratamentos de escuro. Plantas que cresceram em luz solar direta acumularam maior quantidade de biomassa, permitindo o maior desenvolvimento vegetal e produção de inflorescências, contudo capítulos das plantas sombreadas tiveram uma razão central:periférica maior que tratamentos com luz direta. Cipselas de *S. nodiflora* germinam melhor em locais com luz não filtrada, contudo as plantas são adaptadas à condição de sombra. A espécie apresentou um alto potencial germinativo sob uma ampla gama de condições ambientais, assim como rápido desenvolvimento, todas essas características favorecem a distribuição ao longo dos ambientes.

Palavras-chave: aquênio, daninha, potencial osmótico, qualidade de luz, temperatura.

1. Introduction

Diaspore heteromorphism is a common strategy in plant species, which favors seed establishment in a variety of sites, mainly in heterogeneous environments. The morphophysiological differentiation occurs by somatic responses during the diaspore development. The mother plant is capable of directing the resources to a specific diaspore or part of it (Venable and Levin, 1985; Tanowitz et al., 1987; Prinzie and Chmielewski, 1994; Matilla et al., 2005). The Asteraceae presents higher heteromorphic species frequency among the plant families, due to the position of florets in inflorescence (Clavijo, 1995; Imbert, 2002). The morphological differences occur in a pericarp structure, size and color, which influence the species dispersion and establishment directly. Some physiological responses are associated with the external morphological features which improve the success of the strategy (Flint and Palmblad, 1978; Baker and O'Dowd, 1982; Venable and Levin, 1985; Rai and Tripathi, 1987; Clavijo, 2001; van Mölken et al., 2005; Sun et al., 2009).

Some specific environmental conditions are required to start seed germination and abiotic factors, such as temperature, water and light, thus influencing the process. Internal seed controls are responsible for noticing these environmental signs and trigger germination; thereby these control mechanisms can vary between the diaspore types (Flint and Palmblad, 1978). The temperature acts directly in the enzymatic action, which can be annulled or delayed in extreme temperatures, limiting the establishment sites (Venable et al., 1987; Clavijo, 2001). Water is essential for seed metabolism to restart, but the uptake depends on embryo composition, tegument permeability and water availability (Wang et al., 2008). Light signs are perceived by phytochromes, which can induce the germination process, so some seeds are light sensitive. These molecules respond to ratio between the red (660 nm) and the far-red (730 nm) wavelengths, which indicate the light environment surrounding it (Corkidi et al., 1991; Amaral and Takaki, 1998; Ballaré and Casal, 2000). The sum of these abiotic factors creates specific microenvironments, which promotes the germination process. In heteromorphic species, each diaspore type responds to specific conditions, which favors the species to establish in heterogeneous sites (Kingel, 1992).

Heteromorphic cypselas behave with high or low risk factors, which are based on their morphophysiological features. Cypselas present high risks when they are produced in a large number, they have low resources and germinate under variable environments. On the other hand, the low risk strategy presents heavier and dormant diaspores, which only germinate under restrict conditions, normally near the mother plant (Venable et al., 1987; Imbert, 2002). According to the environmental conditions, the mother plant can alter the resource allocation during the diaspore development affecting the quantity and quality of cypselas produced (Flint and Palmblad, 1978; Baker and O'Dowd, 1982; Rai and Tripathi, 1987; Venable et al., 1987; Aarsen and Burton, 1990; Imbert and Ronce, 2001; Donohue et al., 2008). Some weeds have this strategy, which cause a high competitive potential by a wide range time-space establishment. Therefore, the knowledge of these reproduction behaviors is important to plan a management control schedule (Flint and Palmblad, 1978; Tanowitz, et al., 1987; Ballaré and Casal, 2000; Porras and Muñoz, 2000; Kruk et al., 2006).

Synedrella nodiflora is an annual herb species, with life cycles varying between 120 to 150 days. It is common in humid places, shaded and nutrient rich soils and occurs as a weed in many tropical crops. Propagation happens exclusively by dimorphic cypselas: peripheral ones are elliptically shaped with membranous wings from female florets, while the central ones, from monoecious florets, are lanceolate shaped whose pappus are of two stout awns (Kissmann and Groth, 1992). The cypselas germinate differentially under various light quantities and qualities (Ernst, 1906; Marks and Akosim, 1984), while no significant influence was observed for other factors (Chauhan and Johnson, 2009).

Measurement of the cypselas morphology, imbibition rates and germination patterns in *S. nodiflora*, as well as plant growth and reproductive efforts are described in this article. All these features aim to give us important clues as to how this weed behaves, and thereby provides us with a management plan.

2. Material and Methods

Mature *Synedrella nodiflora* capitulum were collected in Rio Claro, SP (22° 23' 44,97" S and 47° 32' 39,92" W) and taken to the Laboratório de Fotomorfogenese de Plantas, where they were stored in impermeable containers, kept in darkness at 7 ± 3 °C. Five hundred cypselas of each type were randomly selected and were digitalized using a high resolution scanner to measure the fruit and awns sizes (Imagetool 3.0). For cypsela mass determination, five replicates of one hundred diaspores were weighed.

Determining the water uptake rates for each cypselas type was done by placing the cypselas inside 70 mm Petri dishes lined with two layers of filter paper moistened with deionized water. Each dish with 100 diaspores were maintained inside germination chambers at 25 ± 1 °C under continuous white light (30 μmol.m^2.s^{-1} approx.) and after 1, 2, 3, 4, 6, 12 and 24 hours the cypselas were removed, dried (with paper towel) and weighed.

The germination tests were done in four replicates of 30 cypselas each inside 70 mm Petri dishes lined with two layers of filter papers imbibed with deionized water or another solution. The dishes were put inside 90 mm Petri dishes and sealed with PVC film to maintain humidity and safety when handling. Fluorescent lamps as a white light source were used over the dishes. For dark treatments, the dishes were put inside dark plastic boxes and the germinated cypselas were recorded in darkness using a dim green safe light. The germination rate index (GRI) was calculated according to Maguire (1962) by daily cypselas germination recording.

Four month stored cypselas were tested for isothermal germination from 10 to 45 °C with 5 °C intervals and ± 1 °C variation. The effect of water potential (0 to -1.2 MPa with -0.2 MPa intervals) on cypsela (eight months stored) germination was done with different concentrations of polyethylene glycol 6000 solutions (Villela et al., 1991) in continuous white light and darkness at 25 ± 1 °C. The effect of different phytochrome photoequilibrium on cypsela germination at 25 ± 1 °C was studied using plexyglass or insulfilm® type filters (Simão et al., 2008) using incandescent bulbs (25 W) as light sources and the dark control. The R:FR ratio of light sources were measured using a LI-1800 (LI-COR, E.U.A.) spectroradiometer and the phytochrome photoequilibrium values (φ) were calculated according to Mancinelli (1994).

For growth experiments *S. nodiflora* plants were submitted to two light treatments to test the light effect in the plant development and cypsela production. Each cypsela type was sown per vase (4.8 L) and the plants were evaluated every thirty days from sowing (DFS) for 150 days. The treated soil consisted of 75% of red latosol from around the *S. nodiflora* population sites and 25% of organic matter, and after chemical analysis, it was observed that the soil was in crop conditions. The vases were placed randomly inside the greenhouse under direct sunlight ($\varphi = 0.61$) and homogeneous shade light simulated by insulfilm® filter ($\varphi = 0.52$). The temperature varied from 7.6 to 34.8 °C according to the season, and the vases were continuously watered.

Every 30 days, ten plants grown from each cypsela type and light treatment were measured for dry mass (dried at 70 °C), total leaf area (Imagetool 3.0) and capitulum numbers produced per plant. The leaf area and the dry mass were used to obtain the leaf area ratio (total leaf area: total plant dry weight). At the end of the experiment, the plant height and dry weight were measured and the numbers of inflorescences were counted. Ten immature capitulum (where all cypselas were still attached) for each plant was selected randomly and the cypselas counted.

The cypselas morphological features and imbibition data were evaluated by the normality test and equal variance test. After having analysed the data for both tests, the one-way ANOVA, followed by Tukey´s test as *post hoc,* was carried out, and when the above mentioned tests failed, the non-parametric ANOVA on ranks was applied. The imbibition curve data were compared using the t-test. The germinability (arc sen $\sqrt{\%}$ transformed) and GRI from isothermal and water potential gradients were analyzed using three-way ANOVA followed by the *post hoc* Tukey´s test for paired comparison of the results. The germinability data (arc sen $\sqrt{\%}$ transformed) from the light gradient experiment were submitted to one-way ANOVA followed by the Tukey's test. For plant growth, regression analyses were made and the tendency line equations were obtained.

3. Results

The central cypselas length, width, weight and awn lengths (0.95 ± 0.14 mm; 4.17 ± 0.30 mm; 67.61 ± 0.82 µg and 3.17 ± 0.69 mm, respectively) were statistically different ($p < 0.05$) of peripheral ones (1.69 ± 0.30 mm; 3.64 ± 0.29 mm; 76.31 ± 1.21 µg and 1.32 ± 0.31 mm, respectively).

The cypselas showed fast imbibition rates, not differing between the types ($p = 0.824$), with the highest imbibition rate happening in the first hour (32.9 ± 3.2%), and after three hours the rate decreased ending the first imbibition phase. The third phase started between 12 and 24 hours when it resumed the cypsela's mass increase and ended with root protrusion.

The *Synedella nodiflora* cypselas germinate in a wide isothermal range from 15 to 40 °C under both light and dark, although the germination rates were higher between 25 to 30 °C, which is considered the optimum temperature range (Figure 1). The variance analysis showed a significance ($p < 0.001$) between the individual factors, such as type, temperature and light effects, with only the interaction between the temperature and light being significant ($p < 0.001$). Under white light, the germinability was higher when compared to darkness for both cypselas types from 20 to 40 °C ($p < 0.001$). The cypselas responses differed under dark treatments ($p < 0.001$), and were more evident at optimum temperatures.

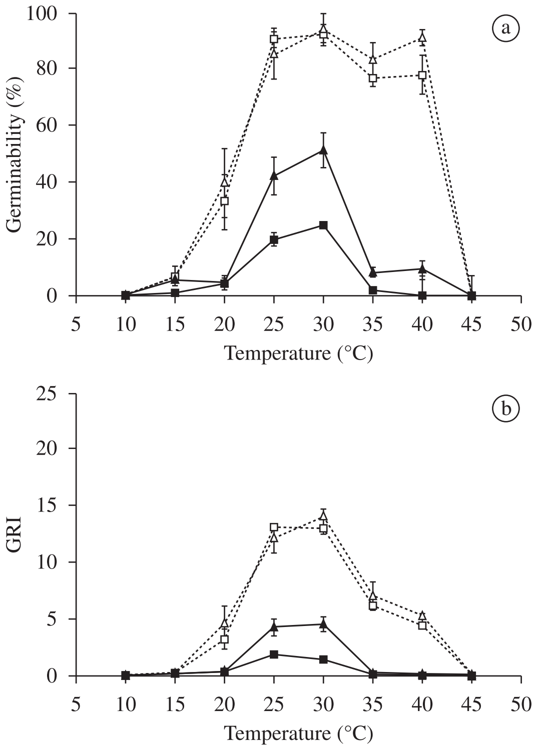


Figure 1. Germinability and Germination Rate Index of central (▲) and peripheral (■) *S. nodiflora* cypselas maintained under isothermal gradient under white light (empty symbol) and darkness (full symbol). Error Bars = Standard Error.

In the water availability experiment, the cypselas germinability decreased after water potential was reduced (Figure 2). There was a significance in all individual factors, such as light and osmotic treatments and cypselas types ($p < 0.001$) analyzed by three-way ANOVA, and the interaction between the three factors had a significant difference ($p < 0.001$). Under continuous white light, the germinability decreased at -0.6 to -0.8 MPa ($p < 0.001$) and at -1.2 MPa there was no germination. Between the cypselas types there were differences only in -0.8 and -1.0 MPa ($p < 0.001$). Under continuous darkness the cypselas germinability was lower than in the light treatment ($p < 0.001$) and was more sensitive to water availability. The germination pattern was different between the cypselas types, the central ones had their germination reduced at -0.2 to -0.4 MPa ($p < 0.001$), while the peripheral decreased at 0 to -0.2 MPa ($p < 0.001$).

The cypselas germinated better at higher phytochrome photoequilibrium (Figure 3). The central type had higher germinability than peripheral at 0.45 ($p = 0.028$), 0.51 ($p = 0.027$) photoequilibrium and in darkness ($p = 0.007$).

Plants grown under direct sunlight accumulated more biomass than plants grown in the shade both in aerial parts as well as in the root, although both lengths were similar (Figure 4, Table 1). This biomass accumulation resulted in more branches and higher capitulum production per plant. The shade grown plants had higher leaf area per dry biomass than light grown ones. At 150 DFS the plants grown under direct light showed the same height as the shade light grown ones, which did not etiolate (Table 1). The capitulum of plants grown in the shade presented a higher amount of cypselas and had a higher proportion of central:peripheral cypselas, although under direct sunlight the plants produced more heads.

4. Discussion

The morphology difference between the cypselas types was clear, influencing its dispersion strategies directly. The central is longer, lighter and its awns are exposed. These features favor the attachment in animal fur; therefore it is carried to farther sites (Rocha, 1996; Brändel, 2004). The peripheral cypselas were heavier, which can be related to additional carbohydrate resources helping in the plant emergence (Chauhan and Johnson, 2009). However, this superior mass could be related to the pericarp wing which may be an alternative structure for dispersion (Brändel, 2007).

Both cypselas imbibition rates followed the same pattern, which indicates no relationship to the germination rate or differences in the fruit coat permeability (Bradford, 1990). The germination responses between the types were not so marked as in another family species, because of a lack of deep innate dormancy in both cypselas types. However, there were some differences between the types of germination rates, which can be related to the environment perception (Baskin and Baskin, 1976; Joley et al., 1997; Imbert, 2002; Brändel, 2004).

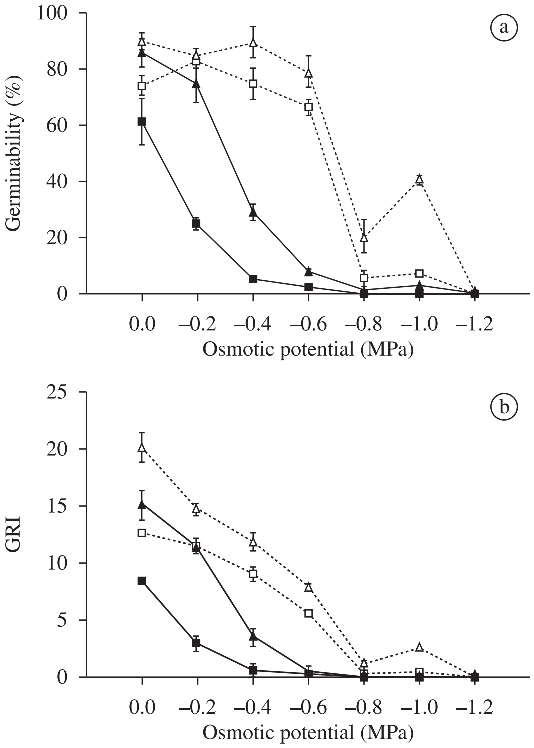


Figure 2. Germinability and Germination Rate Index of central (▲) and peripheral (■) *S. nodiflora* cypselas maintained under osmotic potential gradient (PEG 6000 solutions) under white light (empty symbol) and darkness (full symbol). Error Bars = Standard Error.

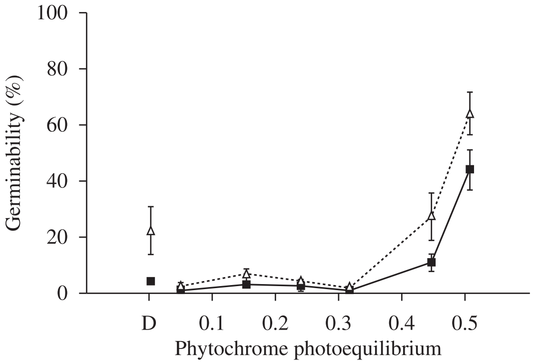
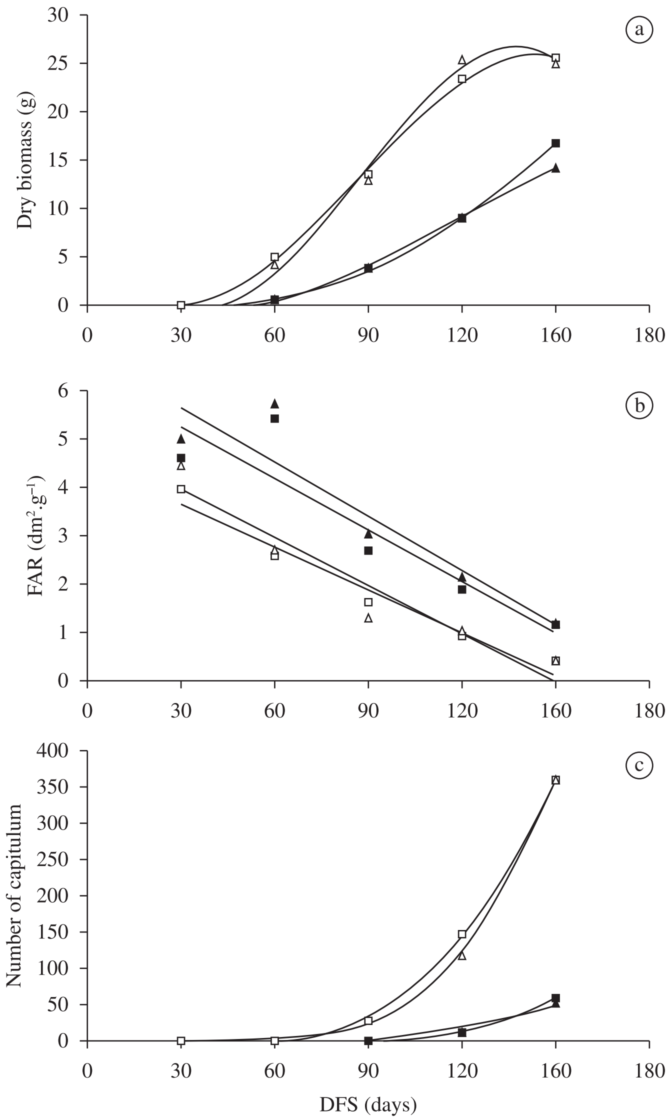


Figure 3. Germinability of central (Δ) and peripheral (■) *S. nodiflora* cypselas maintained under light quality gradient and continuous dark (D) at 25 °C. The phytochrome photoequilibrium value were obtained with different R:FR ratios. Bars on figure = ± Standard Error.

Some heteromorphic cypselas can show different isothermal germination patterns, as in *Heterosperma pinnatum* Cav., in which central cypselas had wider optimum temperature range (Venable et al., 1987). However, both *S. nodiflora* cypselas types germinated in the same pattern



Direct light central:
$y = -5E{-}05x^3 + 0.0142x^2 - 0.8345x + 13.994$
$R^2 = 0.9937$

Direct light peripheral:
$y = -3E{-}05x^3 + 0.009x^2 + 0.4435 + 6.2512$
$R^2 = 0.9986$

Shade central:
$y = -1E{-}05x^3 + 0.0038x^2 - 0.2605x + 4.6889$
$R^2 = 0.9999$

Shade peripheral:
$y = -5E{-}08x^3 + 0.0013x^2 - 0.0976x + 1.7398$
$R^2 = 1$

Direct light central:
$y = -0.0287x + 4.4763$
$R^2 = 0.9639$

Direct light peripheral:
$y = -0.0325x + 4.9081$
$R^2 = 0.9117$

Shade central:
$y = -0.0367x + 6.6887$
$R^2 = 0.8565$

Shade peripheral:
$y = -0.0343x + 6.2109$
$R^2 = 0.8342$

Direct light central:
$y = 0.0004x^3 - 0.0649x^2 + 3.5151x - 58.633$
$R^2 = 0.9995$

Direct light peripheral:
$y = 0.0002x^3 - 0.0148x^2 - 0.0713x + 11.02$
$R^2 = 0.9991$

Shade central:
$y = 0.0068x^2 - 0.8251x + 20.9$
$R^2 = 0.9697$

Shade peripheral:
$y = 0.0001x^3 - 0.0222x^2 + 1.3671x - 2454$
$R^2 = 0.9943$

Figure 4. Plant growth regression analyzes: a) plant dry biomass; b) leaves area ratio; and c) number of capitulum per plant. *S. nodiflora* plants were originated from central (▲) and peripheral (■) cypselas and were submitted to two light growing treatments: direct sun light (empty symbol) and shade (full symbol).

Table 1. Mean data of plant growth and cypsela productions from *S. nodiflora* plants grown for 150 DFS under two light treatments. Measured parameters: aerial parts (A) and roots (R) length (cm) , dry biomass weight (g), leaves area ratio (LAR) (dm^2.g^{-1}), number of capitulum per plant, number of cypselas from ten capitulum of each plant and central:peripheral cypselas ratio. In parenthesis is the mean standard error.

	Length (cm)		**Dry biomass (g)**		**LAR (dm^2.g^{-1})**	**N.º of Capitulum**	**N.º of Cypselas**	**Types ratio**
	R	**A**	**R**	**A**				
Direct sun light	51.51 (1.09)	159.47 (4.16)	3.55a (0.27)	21.67a (0.93)	0.40b (0.03)	362.00a (27.47)	15.15b (0.19)	1.56b (0.05)
Shade light	50.05 (1.20)	171.77 (6.71)	1.61b (0.15)	13.85b (1.01)	1.18a (0.07)	56.25b (4.79)	15.96a (0.30)	1.81a (0.02)

Different letters corresponds to significant difference ($p < 0.05$).

under wide isothermal range that favors the establishment in different sites.

In all germination experiments, *S. nodiflora* cypselas germinate better under white light compared to continuous darkness. This light requirement is frequent among weed species which needs sunlight to trigger germination (Ballaré and Casal, 2000). Furthermore, the degree of this photodormancy can decrease among the storage time (Chauhan and Johnson, 2009) that can be different between the types as shown in *Bidens odonata* Cav. when freshly-harvested cypselas showed different germination rates between the cypselas types, and after one year of storage the germination became similar (Corkidi et al., 1991). Working with *S. nodiflora*, Marks and Akosim (1984) observed that under darkness the peripheral cypselas had higher germination percentages. On the other hand, Ernst (1906) showed that when the light quantity diminished the peripheral germinability reduced, while the central had no effect. These results indicate no predetermined pattern in photodormancy, but the plastic feature. These embryo light responses can be regulated by the mother plant during maturation in reaction to some environmental factors (Aarsen and Burton, 1990; Donohue et al., 2008). The light quality experiment from the present work showed that these embryos are very sensitive to the R:FR ratio in light. As FR amount rises, the germinability decreases, indicating that the process is controlled by phytocrome, where the FR wavelength promotes the photoconversion of Pfr (active molecule) to Pr (inactive) (Rockwell et al., 2006). The present work agrees with Marks and Akosim´s (1984) results, which under green leaf filtered light, the central cypselas germinated more than the peripheral. Under phytochrome photoequilibrium gradient, both *S. nodiflora* cypselas types seem to have the same pattern, however the central had higher germinability than the peripheral ones.

S. nodiflora cypselas were sensitive to low water potentials, observed by early germinability decreases when imbibition water available diminished (Boyd and van Acker, 2004). The germinability pattern at water potential gradient under white light was different from the dark treatment. Under darkness, the germinability was reduced at lower water potential than under white light, thus the embryo under dark treatments seems to be more sensitive to the decrease in the water availability, and the peripheral cypselas appeared to be more sensitive to these conditions than central ones. This happened due to an interaction between the photoreceptors and the water availability, as reported in *Avena fatua* L. (Hsiao and Vidaver, 1971; Boyd and van Acker, 2004). Considering these two limiting factors (water loss and darkness), there was a higher difference in the germination responses between the cypselas types. Consequently, under natural environments, the multiple factors affect the embryo responses in a different way (Joley et al., 1997; Donohue, 2005).

Experimental *S. nodiflora* plants were submitted to few growth limiting factors which allowed a higher growth than natural environment plants, where the maximum length was 80 cm compared to 166 cm average in the present experiment (Kissmann and Groth, 1992). The plant life cycle was extended from 150 days as cited by Kissmann and Groth (1992) to 180 in the present experiment using shade treatments. Plants grown in the shade did not etiolate. In spite of that, there was a higher leaf area under these conditions. The direct sun light treatment was expected to stress the plants, however these plants grew faster than the ones in the shade. Probably natural occurrence under direct light grown plants is limited by another species competition or by water availability.

The cypsela number proportion per capitulum was different, probably because some environmental factors trigger the resource allocation mechanism to a specific cypsela type. Many heteromorphic species in optimum conditions promote central cypselas production for higher fitness (Flint and Palmblad, 1978; Rai and Tripathi, 1987; Venable et al., 1987; Aarssen and Burton, 1990; Clavijo, 2001; Imbert and Ronce, 2001; Benard and McCauley, 2008).

S. nodiflora is a weed characterized by its occurrence in shaded sites, although the diaspore germination in response to light seems to be inconvenient for the establishment. The morphology features of dimorphic cypselas favor spatial dispersion having different strategies which promotes spreading in various sites. On the other hand, germination spreading throughout time seems to be more restricted, since the germination pattern between types are similar. The physiological dimorphism in *S. nodiflora* is related to the germination rates and these differences are important when the environmental conditions are far from the optimum range for the species. The mother plant seems to regulate the proportions, as well as the physiological response pattern of each type based on the environmental conditions, implying a successful establishment strategy.

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